

## Lake Ontario: food web dynamics in a changing ecosystem (1970–2000)<sup>1</sup>

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**Abstract:** We examined stressors that have led to profound ecological changes in the Lake Ontario ecosystem and its fish community since 1970. The most notable changes have been reductions in phosphorus loading, invasion by *Dreissena* spp., fisheries management through stocking of exotic salmonids and control of sea lamprey (*Petromyzon marinus*), and fish harvest by anglers and double-crested cormorants (*Phalacrocorax auritus*). The response to these stressors has led to (i) declines in both algal photosynthesis and epilimnetic zooplankton production, (ii) decreases in alewife (*Alosa pseudoharengus*) abundance, (iii) declines in native *Diporeia* and lake whitefish (*Coregonus clupeaformis*), (iv) behavioral shifts in alewife spatial distribution benefitting native lake trout (*Salvelinus namaycush*), threespine stickleback (*Gasterosteus aculeatus*), and emerald shiner (*Notropis atherinoides*) populations, (v) dramatic increases in water clarity, (vi) predation impacts by cormorants on select fish species, and (vii) lake trout recruitment bottlenecks associated with alewife-induced thiamine deficiency. We expect stressor responses associated with anthropogenic forces like exotic species invasions and global climate warming to continue to impact the Lake Ontario ecosystem in the future and recommend continuous long-term ecological studies to enhance scientific understanding and management of this important resource.

**Résumé :** On trouvera ici un examen des facteurs de stress qui ont modifié profondément l'écosystème du lac Ontario et sa communauté de poissons depuis 1970. Les changements les plus importants ont été la réduction de l'apport de phosphore, l'invasion des *Dreissena* spp., la gestion de la pêche, notamment l'empoisonnement de salmonidés exotiques et le contrôle de la grande lamproie marine (*Petromyzon marinus*), ainsi que la récolte des poissons par les pêcheurs sportifs et les cormorans à aigrette (*Phalacrocorax auritus*). La réaction à ces facteurs a eu pour conséquences: (i) le déclin de la photosynthèse des algues et de la production du zooplancton épilimnétique, (ii) la diminution de l'abondance du gaspateau (*Alosa pseudoharengus*), (iii) la réduction des *Diporeia* indigènes et des grands corégones

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(*Coregonus clupeaformis*), (iv) les modifications comportementales de la répartition spatiale des gaspareaux, ce qui a favorisé les populations indigènes de touladis (*Salvelinus namaycush*), d'épinoches à trois épines (*Gasterosteus aculeatus*) et de menés émeraude (*Notropis atherinoides*), (v) les augmentations spectaculaires de la clarté de l'eau, (vi) les impacts de la prédation des cormorans sur certaines espèces de poissons et (vii) les goulots d'étranglement dans le recrutement des touladis reliés à une déficience de thiamine causée par les gaspareaux. Nous prévoyons que des réactions à des facteurs anthropiques, tels que l'invasion de poissons exotiques et le réchauffement climatique global, continueront à affecter le système du lac Ontario dans le futur et nous recommandons la poursuite d'études écologiques à long terme pour favoriser la compréhension scientifique et la gestion de cette importante ressource.

[Traduit par la Rédaction]

## Introduction

The Laurentian Great Lakes have been subjected to accelerated ecological change since the arrival of European settlers 250 years ago. Lake Ontario and other Great Lakes ecosystems experienced numerous stresses including overfishing, colonization by exotic species, cultural eutrophication, and contaminant discharge leading to degradation in water quality, loss and change of habitat, and the decline of native fish communities in the 1950s and 1960s. By the 1970s, Lake Ontario's major native fish stocks had been pushed to near extinction (Christie 1972). Atlantic salmon (*Salmo salar*), deepwater sculpins (*Myoxocephalus thompsoni*), lake trout (*Salvelinus namaycush*), burbot (*Lota lota*), and coregonids (*Coregonus* spp.) had all disappeared or had seriously declined in abundance, whereas non-native fish like alewife (*Alosa pseudoharengus*), rainbow smelt (*Osmerus mordax*), and white perch (*Morone americana*) proliferated. Overfishing and sea lamprey (*Petromyzon marinus*) predation were considered destabilizing factors in the Lake Ontario fish community. Sea lamprey predation on salmonids and burbot likely increased as the number of dams in the Lake Ontario watershed decreased and acted in concert with commercial fishing to virtually eliminate large piscivores (Christie 1972). Cultural eutrophication, a major destabilizing force of the Lake Ontario ecosystem from the 1940s to the 1970s, led to nuisance algal blooms and water quality deterioration (Schelske 1991).

The sequence of events that led to a deterioration of habitat and fishery stocks throughout the Great Lakes, including Lake Ontario, led to two important milestones. The first was the 1972 Great Lakes Water Quality Agreement (GLWQA) between the United States and Canada, which resulted in controls and permissible phosphorus loadings to each of the Great Lakes and marked a new era of ecosystem management and recovery. The second was the 1971 symposium on Salmonid Communities in Oligotrophic Lakes (SCOL I), which yielded new insights about anthropogenic stressors on fish communities in Great Lakes and comparable ecosystems. SCOL I was an important milestone in the advance of Great Lakes science and was an important stimulus leading to a broader thrust in thinking about fish and fisheries within the context of a lake ecosystem.

Christie (1972) synthesized long-term fish community changes in Lake Ontario and examined abiotic and biotic stressors from the 1800s to 1970 to assess shifts in fish stocks. The lesson learned from Christie's analysis was that although sea lamprey predation, overfishing, and water quality were identified as primary destabilizing factors in the

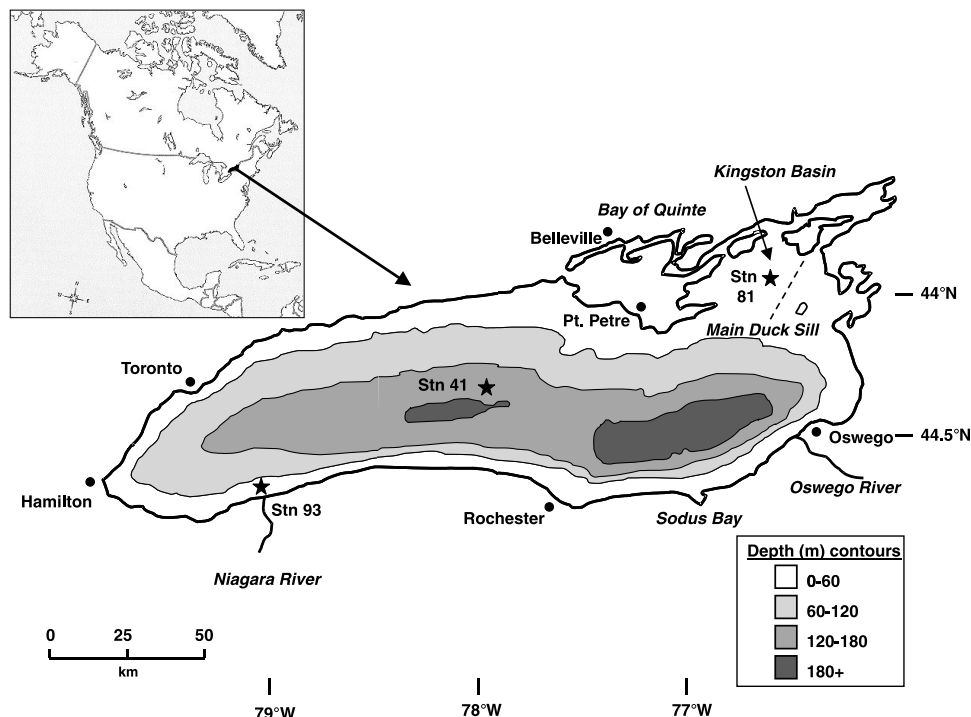
Lake Ontario fish community, a better understanding of food web function was needed. During the 1980s and 1990s, our understanding of the Lake Ontario food web increased, and we realized that exotic fishes, particularly alewife, played a much larger role in the destruction of the original fish community than was previously believed (O'Gorman and Stewart 1999; Ketola et al. 2000). In addition, we now have a greater appreciation for the significant role that humans play as a driving force in shaping the Lake Ontario ecosystem and its food web. Attempts to restore the Lake Ontario ecosystem to historic conditions over the past 30 years through active management to reduce phosphorus, restore native species, and control sea lamprey have been modified by anthropogenic impacts associated with exotic species invasions, habitat modification, and climate change.

In this paper, we build upon the scientific understanding of the Lake Ontario fish community in SCOL I through assessment of the dynamics of the Lake Ontario food web from 1970 through 2000. We hypothesize that although oligotrophication (defined as the reverse of eutrophication) has driven the recovery process of the Lake Ontario ecosystem, the lake will not return to historic conditions but will take a new path in response to unplanned exotic species introductions. Our approach was to analyze available long-term data series on the Lake Ontario food web and to examine anthropogenic stressors that were responsible for ecological and fishery changes in the lake since 1970. We examined the impact of stressors associated with nutrient abatement, exotic species introductions, and fish management on fish communities and species and later speculated on the future of the Lake Ontario ecosystem. In our synthesis and integration of links across trophic levels, we acknowledge the importance of concurrent scientific reviews in a book entitled *State of Lake Ontario: Past, Present, and Future*, edited by M. Munawar (2003), as a source of information. This book originated from a symposium jointly sponsored by the International Association of Great Lakes Research and the Aquatic Ecosystem Health and Management Society.

## The Lake Ontario ecosystem and pivotal events

Lake Ontario (Fig. 1) ranks as the 17th largest lake in the world with a surface area of 18 960 km<sup>2</sup> (Beeton et al. 1999). The lake's watershed is dominated by forests (49%) and agriculture (39%), and 7% of the basin is urbanized (Stewart et al. 1999). Approximately six million people live in the watershed with nearly 70% residing in the province of

**Fig. 1.** Bathymetric map of Lake Ontario showing long-term sampling locations (★).



Ontario. The maximum depth of Lake Ontario's main basin is 244 m, and the relatively shallow Kingston Basin, with its numerous embayments, peninsulas, and islands, accounts for more than 50% of the lake's shoreline. A total of 86% of Lake Ontario's inflow comes from the upper Great Lakes via the Niagara River.

The Lake Ontario ecosystem has been subject to numerous socio-political influences, management actions, and unplanned events since the late 1960s and early 1970s; these events have been crucial to understanding ecosystem changes over the last three decades (Table 1). Pivotal events for Lake Ontario were initially management actions taken to remediate anthropogenic abuses to the aquatic ecosystem and to restore a balanced fish community. The year 1968 saw the first of what was to become annual releases of Pacific salmon to reduce alewife and create a recreational fishery. Large-scale management activities accelerated through the 1970s with the signing and implementation of binational agreements to reduce phosphorus loading to the lake, the initial treatment of streams tributary to Lake Ontario to kill larval sea lamprey, and the start of annual releases of hatchery-reared lake trout for population restoration. However, the pivotal event for the ecosystem in the 1990s was not a planned, science-based, management action but rather was the unintentional establishment and proliferation of a suite of exotic species from Eurasia that gained entry to the Great Lakes in association with transoceanic shipping.

### Nutrient dynamics and oligotrophication

Mandated programs to control phosphorus in the Great Lakes and Lake Ontario were an undeniable success (Stevens and Neilson 1987; Millard et al. 2003) and initiated the process of oligotrophication. Phosphorus loading to Lake Ontario declined

by nearly 50% from a peak of 15 036 tonnes (t)·year<sup>-1</sup> in 1969 to 7410 t·year<sup>-1</sup> by 1981, close to the loading target of 7000 t·year<sup>-1</sup> established in the GLWQA (International Joint Commission 1988; Fig. 2a). Spring total phosphorus (TP) concentrations declined by over 50% from 20–25 µg·L<sup>-1</sup> in the early 1970s to just below the target concentration of 10 µg·L<sup>-1</sup> by 1986 (9.9 µg·L<sup>-1</sup>). From 1986 to 1993, TP concentrations fluctuated within ±0.5 µg·L<sup>-1</sup> of the target of 10 µg·L<sup>-1</sup>. This recovery period (12 years) was consistent with early phosphorus models (Chapra and Sonzogni 1979) suggesting that the response time for Lake Ontario to achieve target concentrations resulting from phosphorus control measures would range from 8 to 22 years.

In contrast to phosphorus (P), silica exhibited no long-term changes in the open waters of Lake Ontario (Johannsson et al. 1998; Millard et al. 2003), whereas nitrate concentrations as nitrate increased significantly, especially from 1968 to 1987 (Millard et al. 2003; Fig. 2b). Mean spring nitrate concentrations nearly doubled from 215 µg·L<sup>-1</sup> in 1968 to about 400 µg·L<sup>-1</sup> by the late 1980s but leveled off during the 1990s (Stevens and Neilson 1987; Lean 1987; Neilson et al. 1994). Lean (1987) concluded that the increase in nitrate was associated with higher loading from the watershed and was not associated with reduced algal demand because the nitrate increase occurred before implementation of phosphorus control. Millard et al. (2003) showed that the rate of nitrate increase paralleled nitrogen (N) fertilizer use in the Great Lakes basin and mirrored the observed Lake Ontario mid-lake increase up to the mid-1980s.

Ratios of N to P in the early 1970s (Stevens and Neilson 1987) were in the range (16:1) where N and P might have co-limited phytoplankton growth (Forsberg et al. 1978; Vincent 1981). However, the steady increase in nitrate and decrease in TP over the last two decades has elevated the N:P in excess of 50:1 (Johannsson et al. 1998), which suggests

**Table 1.** Management actions, socio-political influences, and unplanned events that have been pivotal to understanding ecological changes in the Lake Ontario ecosystem since 1968.

Year	Pivotal event	Citation
1968	First annual release of Pacific salmon for alewife control and recreational fishing	Owens et al. 2003
1970	Canada limits phosphates in detergents	Stevens and Neilson 1987
1971	First treatment of Canadian tributaries to Lake Ontario with lampricide	Pearce et al. 1980
1972	New York limits phosphates in detergents	Stevens and Neilson 1987
1972	U.S.–Canada Great Lakes Water Quality Agreement sets in motion programs to control P discharges	Stevens and Neilson 1987
1972	First treatment of New York tributaries to Lake Ontario with lampricide	Pearce et al. 1980
1973	First annual release of hatchery lake trout for population restoration	Elrod et al. 1995
1974	Twenty-two cormorant nests on Little Galloo Island	Weseloh and Ewins 1994
1982	First record of fry produced in lake by hatchery lake trout	Marsden et al. 1988
1983	Last record of bloater	Owens et al. 2003
1989	First record of zebra mussel	T. Schnaer, Ontario Ministry of Natural Resources, Glenora Fisheries Station, Picton, ON K0K 2T0, personal communication
1991	First record of quagga mussel	Mills et al. 1993
1992	Start of <i>Diporeia</i> collapse	Lozano et al. 2001
1993	Start of annual, successful reproduction by hatchery lake trout	O’Gorman et al. 2000
1995	First record of blueback herring	Owens et al. 1998
1996	First record of <i>Echinogammarus ischnus</i>	Dermott et al. 1998
1998	First record of <i>Cercopagis pengoi</i>	MacIsaac et al. 1999
1998	First record of round goby ( <i>Neogobius melanostomus</i> )	Owens et al. 2003

that Lake Ontario is more P-limited (Forsberg et al. 1978; Vincent 1981) for at least 3 months during the summer in the open deep waters of the lake (Lean et al. 1987; Millard et al. 1996a). The shallow Kingston Basin is P-limited for a much longer period than the offshore habitat because spring water column light intensities can exceed growth-limiting levels at full vertical mixing in this part of the lake, but not offshore (Millard et al. 1996a).

### Phytoplankton dynamics, primary production, and the microbial loop

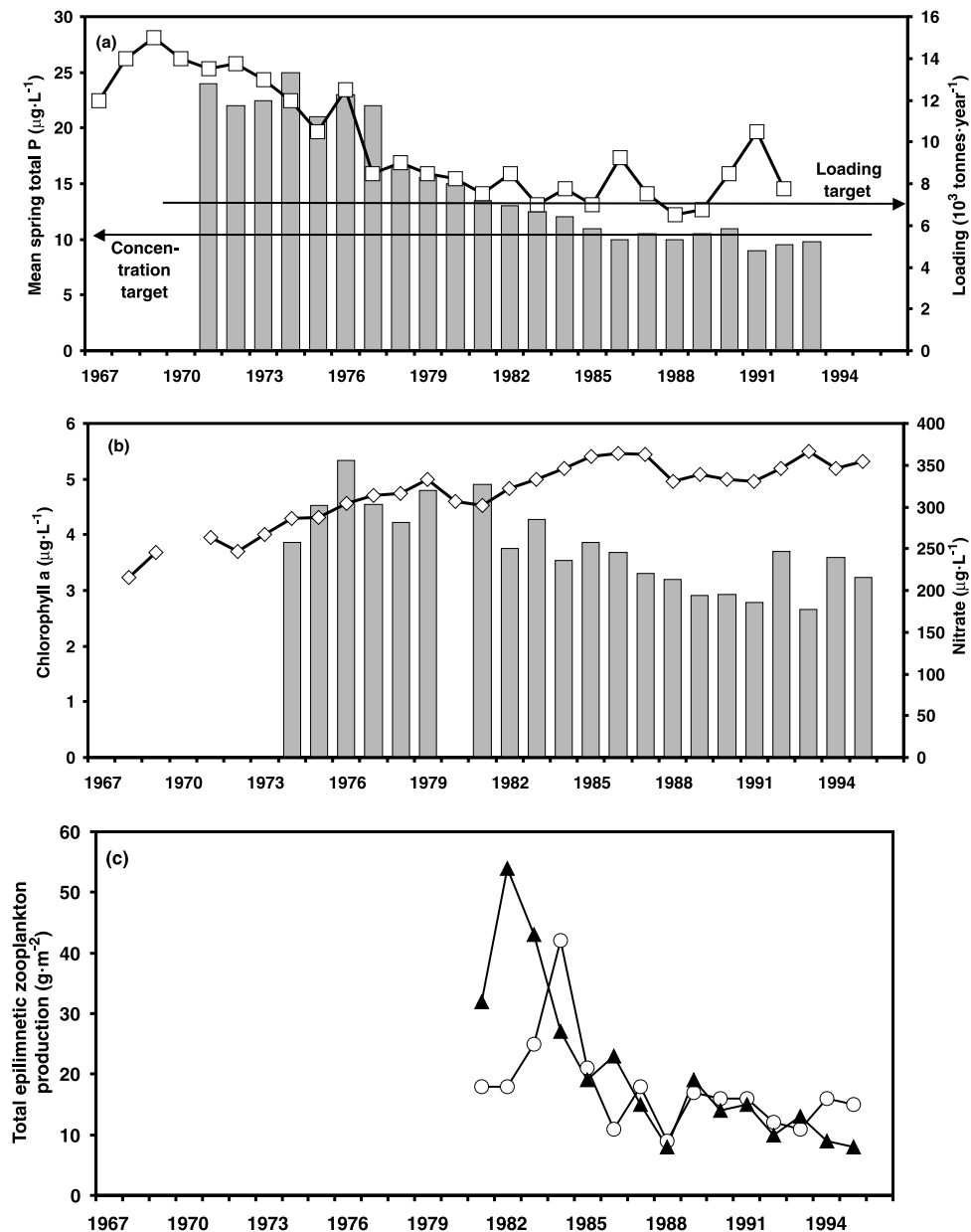
Phytoplankton dynamics in Lake Ontario since 1970 reflected shifts toward oligotrophy. Comparison of lakewide surveys conducted in 1970 (high phosphorus) and 1990 (low phosphorus) showed an increase of oligotrophic over eutrophic species (Vollenweider et al. 1974; Munawar and Munawar 1996; Munawar et al. 2003). Predominant eutrophic species of diatoms and cyanobacteria have either been replaced by oligotrophic species or occur in very low numbers, and the relative abundance of oligotrophic species of diatoms and chrysophytes has increased. Other shifts in phytoplankton dynamics in response to the invasion by *Dreissena* spp. in 1989 might be anticipated, but lakewide responses remain largely unknown.

Summer phytoplankton growth in Lake Ontario has probably always been P-limited, even at the higher concentrations before P control (Lean et al. 1987; Millard et al. 1996a). However, algal biomass, as indicated by summer chlorophyll (Chl), did not respond immediately to reduced P loadings and concentrations. Lakewide Chl did not decline until the

early 1980s when a decrease of about  $2 \mu\text{g}\cdot\text{L}^{-1}$  was observed between 1976 and 1985 (Stevens and Neilson 1987; Millard et al. 2003); Chl remained at these lower levels ( $2.5\text{--}3.5 \mu\text{g}\cdot\text{L}^{-1}$ ) between 1985 and 1993 (Fig. 2b). Summer Chl concentrations declined in the Kingston Basin from maxima of  $5.0\text{--}6.0 \mu\text{g}\cdot\text{L}^{-1}$  in the early to mid-1980s to  $3.5\text{--}4.5 \mu\text{g}\cdot\text{L}^{-1}$  through the late 1980s and 1990s. The recent spring (pre-stratified) Chl decline in the Kingston Basin was particularly evident after 1992, in spite of stable TP concentrations during this time (Millard et al. 2003). The significance of the Chl decline in the 1990s was that it occurred in the Kingston Basin and not in offshore waters of the open lake.

Studies of primary productivity (PP) in freshwater lake ecosystems have generally correlated seasonal or annual changes in PP with P loading (Millard and Johnson 1986). In Lake Ontario, seasonal areal phytoplankton photosynthesis (1 May to 31 October) declined by 30% coincident with the decline in P concentrations for the period 1972 to 1992 (Millard et al. 1996b). However, the observed decline in algal photosynthesis was not proportional to the 50% decline in Lake Ontario phosphorus concentrations because of the positive compensating effect that increased light penetration has on depth of photosynthesis. Light penetration and deepening of the euphotic zone increased further in the 1990s following establishment of *Dreissena* spp. In the Kingston Basin, for example, the extinction coefficient of photosynthetically active radiation ( $E_{\text{PAR}}$ ) declined 25% from a seasonal mean of  $0.35 \text{ m}^{-1}$  in 1991 to  $0.26 \text{ m}^{-1}$  in 1994–1995; this equates to a deepening of the euphotic zone by about 5 m. In spite of this increase in light penetration, areal photosynthetic rates have not likely been maintained at the same

**Fig. 2.** (a) Long-term trends in phosphorus loading ( $\square$ ) and mean spring total phosphorus concentrations (bars) (spring surveillance cruises) in Lake Ontario (from Millard et al. 2003). (b) Long-term trends in mean summer chlorophyll *a* (bars) and mean spring nitrate ( $\diamond$ ). Values represent combined means from Bioindex stations 41 and 81 and from surveillance cruises. (c) Trends in total epilimnetic zooplankton production between 15 June and 31 October. Estimates based on samples collected from either the top 20 m or the epilimnion of Lake Ontario, whichever was shallower, at stations 41 ( $\circ$ ) and 81 ( $\blacktriangle$ ) of the Bioindex program.



levels as observed before dreissenid mussel invasion unless there has been a drastic increase in photosynthesis per unit biomass of algae (Millard and Sager 1994).

Lakewide studies of size-fractionated primary production in Lake Ontario from 1990 to 1997 reflect periods of post-phosphorus reduction and post-dreissenid establishment (Munawar and Munawar 2003). Except in the spring of 1990, the bulk of primary production has been associated with smaller-sized nanoplankton (2–20  $\mu\text{m}$ ) and picoplankton ( $<2 \mu\text{m}$ ). The importance of smaller-sized fractions contributing to Lake Ontario's pelagic primary production in the 1990s has likely been a major change from the presumed higher netplankton contribution to overall algal

production during the eutrophic period of the early 1970s (Vollenweider et al. 1974). Although there are no size-fractionated primary production estimates from Lake Ontario in the early 1970s, estimates in nearby Lake Erie indicated that netplankton contributed to the bulk of primary production at that time (Munawar and Burns 1976).

Our understanding of the Lake Ontario food web in 1970 did not include knowledge of the microbial food web (MFW), which includes bacteria, heterotrophic nanoflagellates, ciliates, nanoplankton, and picoplankton (Munawar et al. 2003). The MFW is now considered an essential pathway of energy transfer to zooplankton (Munawar and Munawar 1999). Heterotrophic flagellates and bacteria are active in biodegradation

of organic material that regenerates mineral substances, which are consequently used by unicellular autotrophs. In turn, flagellates are consumed by microzooplankton such as ciliates (10–80  $\mu\text{m}$ ). With the shift toward a more oligotrophic state, we can only speculate that the plankton community has shifted toward autotrophic nanoplankton and picoplankton with a tight coupling between heterotrophic nanoflagellates and bacteria (Munawar et al. 2003).

## Zooplankton dynamics and production

The shift toward oligotrophy of the Lake Ontario ecosystem was expected to impact the zooplankton community composition through a reduction in eutrophic species. Whole-lake, large-scale studies in the late 1960s and early 1970s (Patalas 1969, 1972) revealed that the zooplankton community was dominated by small cladocerans and cyclopoid copepods, primarily *Diacyclops thomasi* (formerly *Cyclops bicuspidatus thomasi*), *Tropocyclops extensus* (formerly *T. prasinus mexicanus*), *Bosmina* spp. (*B. leidei* and *B. freyi* formerly known as *B. longirostris*), and *Daphnia retrocurva*. Mesotrophic and eutrophic zooplankton species such as *Eubosmina coregoni* and *Ceriodaphnia lacustris* were present regularly, whereas *Chydorus sphaericus*, *Eurytemora affinis*, *Acanthocyclops vernalis*, *Leptodora kindtii*, and *Mesocyclops edax* were seen only occasionally (Makarewicz 1993; Johannsson et al. 1998). This community remained intact through the 1980s (Johannsson et al. 1991). The response of the zooplankton community to phosphorus reductions, however, was subtle. *Chydorus sphaericus* disappeared in the early 1990s, and *Ceriodaphnia lacustris* declined in abundance and was not observed in the mid-lake in 1995 (Johannsson 2003).

The impact of alewife on the zooplankton species composition since the early 1970s in Lake Ontario has been significant, and intense planktivory by these fish has structured the zooplankton community toward small species (e.g., *Bosmina*). Zooplankton are the principal food of juvenile and adult alewife (Mills et al. 1992; Urban and Brandt 1993), and alewife were responsible for >96% of the predation on zooplankton by Lake Ontario fish as late as 1990 (Rand et al. 1995). Alewife abundance declined 42% from the early 1980s to the early 1990s (O'Gorman et al. 2000), and subtle changes were observed in the zooplankton community coincident with this decline. Observed changes included an increase in abundance of larger zooplankton species, and August mean cladoceran length was larger in 1990–1991 than in the late 1980s (Johannsson 2003). Relative production of *Daphnia* increased from <15% (1981–1985) to 30–50% (1986–1995) of total zooplankton production (Johannsson 2003); over this period, the abundance of summer cyclopoid copepods (1987–1995 in the mid-lake) and of total zooplankton (in the spring over the 1981–1995 period) also increased (Johannsson et al. 1998). Decreases in planktivory should have led to detectable increases in zooplankton productivity; however, no significant increase in zooplankton production was observed between 1987 and 1995 (Johannsson et al. 1998; Johannsson 2003). To the contrary, zooplankton production declined significantly between 1981 and the early 1990s in the main lake, along the south shore, and in the Kingston Basin and paralleled the decline in TP concentrations (Johannsson et

al. 1991, 1998; Johannsson 2003; Fig. 2c). In the mid-lake, epilimnetic zooplankton production declined from 17–42 g dry weight (dw)·m<sup>-2</sup>·season<sup>-1</sup> (season = 15 June – 31 October) between 1981 and 1985 to 8–19 g dw·m<sup>-2</sup>·season<sup>-1</sup> from 1986 to 1995. In the Kingston Basin, zooplankton production declined from 28–52 g dw·m<sup>-2</sup>·season<sup>-1</sup> between 1981 and 1984 to 7–13 g dw·m<sup>-2</sup>·season<sup>-1</sup> between 1993 and 1995. The decline in zooplankton production in association with declines in phosphorus led Johannsson (2003) to rule in favor of nutrient decline instead of fish zooplanktivory as the driving force leading to lower zooplankton production in Lake Ontario in the 1980s and early 1990s.

The zooplankton web has become more complex since 1970 with the addition of two exotic spiny-tailed cladocerans and veliger larvae of *Dreissena* spp. The cladoceran *Bythotrephes longimanus* (formerly known as *B. cederstroemi*) was first seen in 1982, and *Cercopagis pengoi* was first observed in 1998 (MacIsaac et al. 1999). Both *B. longimanus* and *C. pengoi* are predators on other zooplankton; recent evidence by Benoit et al. (2002) indicates that *C. pengoi* feeds on small copepods and *Bosmina* and likely decreases juvenile copepod production through direct predation and a shift of copepod vertical distribution to deeper, colder waters. Interestingly, *B. longimanus* has only been observed in Lake Ontario in 1987 and 1994 (primarily in the fall), whereas *C. pengoi* has been observed lakewide since 1998 (highest densities in August and September) (Makarewicz et al. 2001). At present, *B. longimanus* has little impact on food resources of fish. *Cercopagis*, on the other hand, is very abundant in the summer and its impact on fish is currently unknown.

*Mysis relicta*, an abundant omnivore with important links in Lake Ontario's benthic and pelagic food web, is a dominant prey of rainbow smelt and a common prey of alewife and slimy sculpin (*Cottus cognatus*) (Owens and Weber 1995). Interestingly, mysid population densities have remained relatively stable since the mid-1980s despite shifts toward oligotrophy and reductions in zooplankton production (Johannsson et al. 2003). However, mysid production in the offshore (1984–1995) increased with declines in alewife predation in the 1990s (Johannsson et al. 2003).

## The benthic macroinvertebrate community

With mandated binational programs to improve water quality conditions in Lake Ontario in the 1980s and 1990s, expectations were high that the benthic community would benefit greatly from these efforts, but unfortunately, toxic contaminants in Lake Ontario sediments have dampened such expectations leading to a decline in certain pollution-sensitive species. For example, studies by Nalepa and Thomas (1976) and Barton and Anholt (1997) both found that pollution-sensitive *Diporeia* were rare at sites near the mouth of the Niagara River. Such scarcity has been attributed to high loadings of chlorinated hydrocarbons from industries (Durham and Oliver 1983; Nalepa 1991).

One of the most significant changes in the benthic macrofauna of Lake Ontario has been the establishment of two species of *Dreissena*. The zebra mussel, *Dreissena polymorpha*, was first detected in the lake in 1989, and by 1991, *Dreissena bugensis* (also known as the quagga mussel) was observed co-

existing with the zebra mussel (Mills et al. 1993). South-shore studies between 1992 and 1995 showed that total *Dreissena* biomass had increased and that areas of lake bottom dominated by zebra mussels in 1992 were dominated by quagga mussels in 1995 (Mills et al. 1999). Associated with the dramatic increase in *Dreissena* spp. was a collapse of the larger fingernail clams (*Sphaerium* spp., mainly *S. corneum* and *S. nitidum*; Fig. 3a); this collapse was likely due to competition with *Dreissena* for food and space. Coincident with the ascent of *Dreissena* spp., numbers of the shallow water amphipod *Gammarus fasciatus* increased, perhaps because they benefitted from the structural complexity associated with mussel colonies and the energy transfer to the benthos through pseudofecal deposition (Stewart and Haynes 1994; Haynes et al. 1999). However, *Gammarus* may be replaced in the future by the newly established amphipod *Echinogammarus ischnus*; by 1996, *E. ischnus* was present at the mouth of the Niagara River, where it displaced *Gammarus fasciatus* (Dermott et al. 1998). Colonization of Lake Ontario by the filter-feeding *Dreissena* spp. has likely decreased crustacean zooplankton production, particularly in nearshore (defined as <30 m depth) regions, if the ecological response is similar to that of Lake Erie, where dreissenid mussels depressed zooplankton production through their impact on pelagic primary production (Johannsson et al. 2000). Finally, the nearshore macrobenthos community has undergone further change with the replacement of the gastropod snails *Amnicola* spp. and the *Valvata* spp. with the exotic New Zealand mud snail (*Potamopyrgus antipodarum*; Zaranko et al. 1997).

Historically, the burrowing amphipod *Diporeia* represented 60–80% of benthic biomass in Lake Ontario (Johannsson et al. 1985) and was critically important as a food source for lake whitefish (Hoyle et al. 2003). In the Kingston Basin, density of *Diporeia* increased between 1983 and 1989 and reached a seasonal average just over 13 000·m<sup>-2</sup> in 1988 (Fig. 3b). Dry biomass ranged from 2.3 to 3.0 g·m<sup>-2</sup> before 1985 (Johannsson et al. 1985; Dermott and Corning 1988) and peaked at 5.0 g·m<sup>-2</sup> in 1988. A rapid population increase of *Diporeia* between 1987 and 1989 in offshore waters was in synchrony with similar events in the Kingston Basin (site 81) and in the Bay of Quinte (Dermott 2001). After 1990, *Diporeia* density in the Kingston Basin (at depths <35 m) plummeted to <4·m<sup>-2</sup> by October 1995 and to zero in April 1996 (Fig. 3b; Dermott 2001). Lozano et al. (2001) also observed a significant decline in *Diporeia* density between 1972 and 1997 at depths of 12–88 m. A zone of low *Diporeia* density (<4 individuals·m<sup>-2</sup>) encompassing a significant portion of the soft sediment habitat in Lake Ontario currently extends to 26 km offshore and as deep as 160 m (Lozano et al. 2001). This reduction of *Diporeia* is expected to have a significant impact on the fish of Lake Ontario that are dependent on these organisms for their growth and survival.

## Fish community dynamics

Fish managers recognized the numerous stresses on the Lake Ontario fish community before the 1970s and instituted new measures to set the stage for the recovery process. Most notable were sea lamprey control (Pearce et al. 1980), quotas to regulate commercial fishing effort, and stocking of salmonid

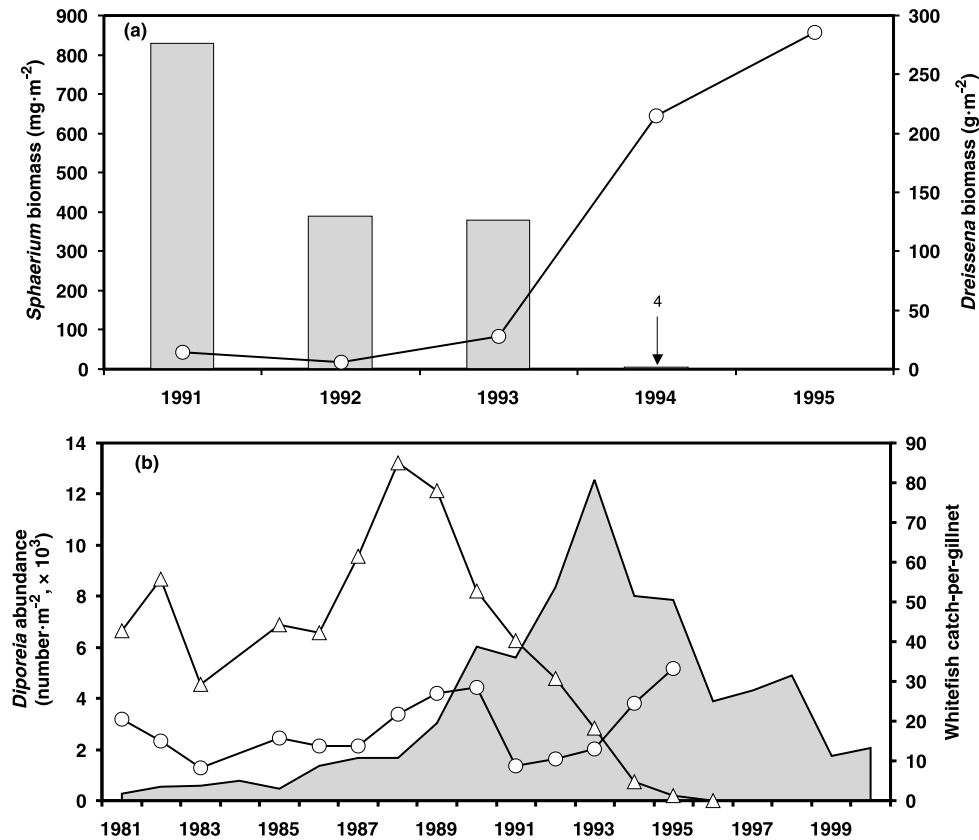
predators to control exotic prey fish like alewife (Christie et al. 1987a). Further control measures included efforts to minimize loadings of mercury, chlorinated hydrocarbons of DDT (dichlorodiphenyltrichloroethane) and PCBs (polychlorinated biphenyls), and municipally produced phosphorus (Minns et al. 1986). The full effects of these initiatives on Lake Ontario fish were not expected to be known until the 1980s and 1990s.

In the early 1970s, efforts to control nuisance levels of alewife, to establish a sport fishery, and to restore lake trout led to an acceleration of stocking of fish predators including lake trout, brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), Atlantic salmon, chinook salmon (*O. tshawytscha*), and coho salmon (*O. kisutch*). Limited stocking of kokanee salmon (*O. nerka*) during 1965–1972 was not successful and was discontinued in 1973 (Pearce et al. 1980). These introductions initially failed to produce significant fisheries because of high parasitic sea lamprey-induced mortality (Pearce et al. 1980). Sea lamprey control was initiated in 1971, and by the mid-1980s, stocks of lake trout, brown trout, chinook salmon, and coho salmon all responded positively to reduced numbers of parasitic lamprey. These successes led to a new set of management issues — what is the most suitable fish species mixture for the lake and what level of stocking is necessary to maintain a balance between predator demand and prey fish supply?

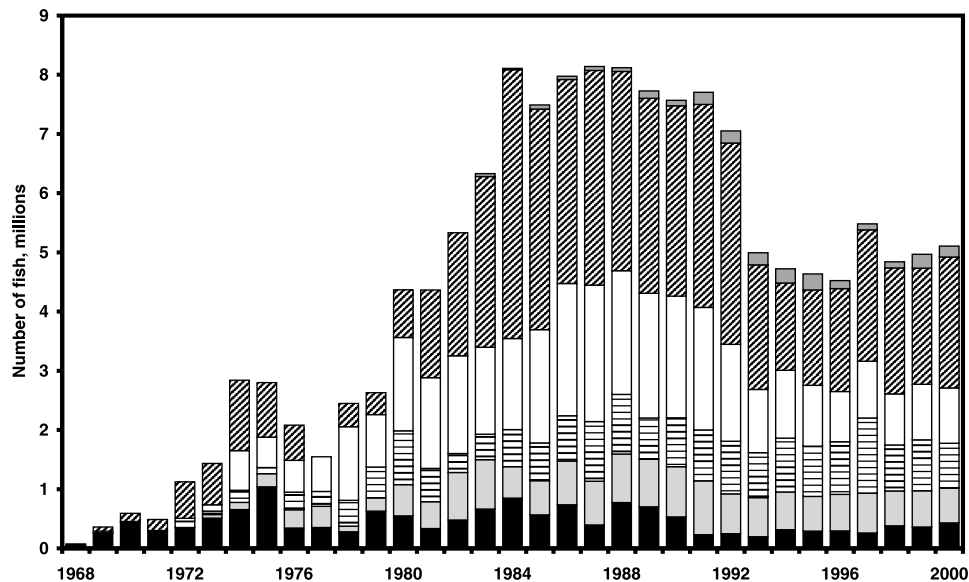
Enhanced survival of trout and salmon led to an expansion of hatchery stocking programs in both New York and Ontario and the dawn of a massive recreational fishing industry (O’Gorman and Stewart 1999). Pacific salmonines played a pivotal role in the transformation of the recreational fishery. As the salmonid fishery expanded with the onset of accelerated stocking efforts (beginning in 1980) and the potential for record fishery yields was eminent, management concerns emerged about the sustainability of the salmonid fishery with a waning alewife population (O’Gorman and Stewart 1999). By the mid-1980s, the state of New York and the province of Ontario agreed to limit stocking to 8 million salmonids (including chinook, coho, and Atlantic salmon and lake, rainbow, and brown trout) annually (Fig. 4; Kerr and Le Tendre 1991). The outcome of these efforts to rehabilitate the Lake Ontario fishery resulted in a multimillion dollar recreational fishing industry (O’Gorman and Stewart 1999). Total annual expenditures by anglers participating in Lake Ontario’s recreational fisheries were impressive; expenditures were \$53 million (Canadian) for the province of Ontario in 1995 (Department of Fisheries and Oceans 1997) and \$71 million (U.S.) for New York in 1996 (Connelly et al. 1997). Concerns about salmonid predator demand and prey supply were rekindled in the early 1990s (Jones et al. 1993); by 1993, salmonid stocking levels were reduced to 4.5 million and since have been maintained at between 4 and 5.5 million annually (Fig. 4).

Development of a world-class salmonid fishery produced tremendous fishing harvest and effort by anglers. Harvest also reflected angler preference — chinook salmon were most sought after by anglers, followed by rainbow trout, lake trout, brown trout, and coho salmon (Stewart et al. 2003). Harvest rate declined from 1985 to 1995 and the reduction in salmonid stocking was followed by declines in

**Fig. 3.** (a) Shell-free dry weight biomass in October of *Sphaerium* (bars) and *Dreissena* (○) at a sandy-silt inshore site (station 93) in Lake Ontario, 1991–1995. (b) Yearly mean density of the amphipod *Diporeia* at Bioindex stations 41 (○) and 81 (△) in Lake Ontario, 1981–1996, and catch-per-gillnet (shaded area; sum of catch adjusted to 100 m of each mesh size, 3.8- to 15.2-cm stretch measure) of age-1 and older lake whitefish in the Kingston Basin of Lake Ontario, 1981 to 2000.



**Fig. 4.** Numbers of coho salmon (*Oncorhynchus kisutch*; solid), brown trout (*Salmo trutta*; light shading), rainbow trout (*Oncorhynchus mykiss*; horizontal hatching), lake trout (*Salvelinus namaycush*; open), chinook salmon (*Oncorhynchus tshawytscha*; diagonal hatching), and Atlantic salmon (*Salmo salar*; dark shading), stocked in Lake Ontario, 1968–2000 (excludes fish stocked at a weight <1 g).



fishing effort. By 1995, fishing effort declined to about half of the 1990 peak and harvest declined by two- to four-fold for all species from 1985 to 1995.

In the 1970s and early 1980s, Lake Ontario's offshore fish

community was dominated by non-native planktivores (alewife and rainbow smelt) and a native benthivore, slimy sculpin (Owens et al. 2003). By the 1990s, exotic planktivores declined as did slimy sculpins, but native fishes



like threespine stickleback (*Gasterosteus aculeatus*) and emerald shiner (*Notropis atherinoides*) became more common.

### Alewife

The Lake Ontario fish community had massive numbers of alewife in the decades before 1970, and fishery biologists recognized the need to develop indices of alewife abundance (O'Gorman and Stewart 1999; Owens et al. 2003; Casselman and Scott 2003). A mass mortality of alewives during the winter of 1976–1977, precipitated by unusually cold temperatures, depressed alewife numbers during the late 1970s (O'Gorman and Schneider 1986; Bergstedt and O'Gorman 1989). Following the 1976–1977 mass mortality, bottom trawl catches showed alewife numbers increasing in both the Kingston Basin and U.S. waters (Fig. 5). In the 1980s, the number of alewives in the Kingston Basin during summer gradually rose, whereas the number of alewives in U.S. waters of the lake in spring slowly declined. In the early 1990s, alewife numbers spiked sharply in the Kingston Basin but remained stable in U.S. waters. By the late 1990s, alewife numbers were at very low levels in both regions of the lake. Heavy fish predation was one likely factor causing reduction in alewife numbers in the lake during the late 1990s, but perhaps more important was the absence of a strong year-class during 1992–1997. Year-class strength was judged from catches of age-1 fish in spring bottom trawls in U.S. waters. Of the six year-classes produced during 1992–1997, two were the smallest produced during 1977–1997, one was the sixth smallest produced, and two were close to the long-term average. The waning population of alewife posed a new problem for fishery managers. Because the alewife fueled an economically important recreational fishery, managers recognized that they must conserve the diminished alewife population to preserve the recreational fishery.

Alewives are both primary prey of salmonines and important predators on zooplankton (Urban and Brandt 1993), larval fish (Krueger et al. 1995; Mason and Brandt 1996), and macrozooplankton (*Bythotrephes* and *Mysis*; Mills et al. 1992). Zooplankton stocks, juvenile alewife abundance and growth, and growth of young salmonines were tightly linked. O'Gorman et al. (1987) found that first-year growth of coho salmon did not depend on size at release but was related to the biomass of age-0 alewives, whereas second-year growth of coho salmon depended on biomass of yearling alewife (O'Gorman et al. 1987). In Lake Ontario, growth of age-1 alewives during 1984 to 1991 was slower than that in Lake Michigan during the 1960s and Lake Huron during the 1970s, when alewives were an important forage species in the fish communities of those two lakes. Growth of age-1 alewives in Lake Ontario was dependent on epilimnetic zooplankton density and the number of competing age-0 alewives (O'Gorman et al. 1997). Consequently, the link of the youngest cohorts of alewife to zooplankton is important, as these fish represent the bulk of alewife production in Lake Ontario and are critical to supporting a substantial piscivore sport fishery.

### Rainbow smelt

Rainbow smelt are the second most abundant open-water fish in Lake Ontario (Casselman and Scott 2003) and feed on a variety of food resources including zooplankton, non-native

macrozooplankton (e.g., *Bythotrephes*), macroinvertebrates (e.g., *Mysis* and *Diporeia*), and larval and juvenile fish (O'Gorman 1974). Numbers and biomass of rainbow smelt fluctuated widely and without trend in U.S. waters of Lake Ontario during 1978–1998 (Fig. 6). The most dramatic change in the rainbow smelt population was the marked decline in large rainbow smelt that was evident by the mid-1980s. Christie et al. (1987a), Casselman and Scott (1992), and Owens et al. (2003) all considered size-selective predation by salmonids as the most plausible explanation for the reduction of large rainbow smelt.

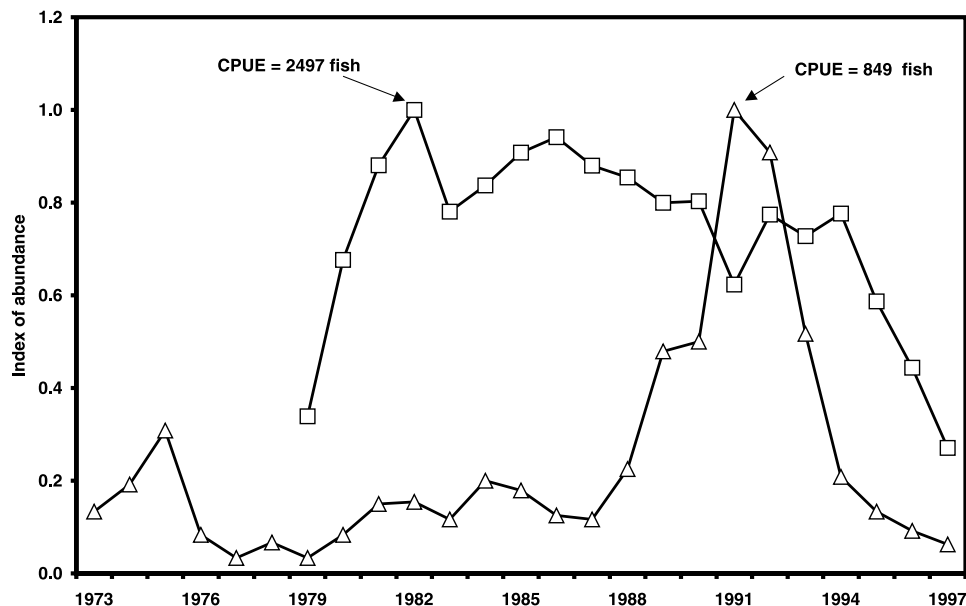
### Slimy sculpins

Slimy sculpins are native benthic fish and are important to the diet of lake trout (Elrod and O'Gorman 1991). Numbers of slimy sculpins fell sharply in southern Lake Ontario between fall 1982 and fall 1984 because of predation by stocked juvenile lake trout (Owens and Bergstedt 1994). Numbers slowly rose from 1984 to 1991, declined abruptly in 1992, and remained low during 1993–1998 in both U.S. and Canadian waters (Casselman and Scott 2003; Owens et al. 2003). The 1992 decline in overall numbers was due entirely to the collapse of the dense population of poor conditioned, slow-growing fish in the southeast corner of the lake at depths >70 m (Owens and Weber 1995; Owens and Noguchi 1998). Owens et al. (2003) hypothesized that the decline of slimy sculpins was due to reductions in productivity brought on by nutrient abatement and to reductions in *Diporeia*, an important food of slimy sculpin, brought on by *Dreissena* colonization.

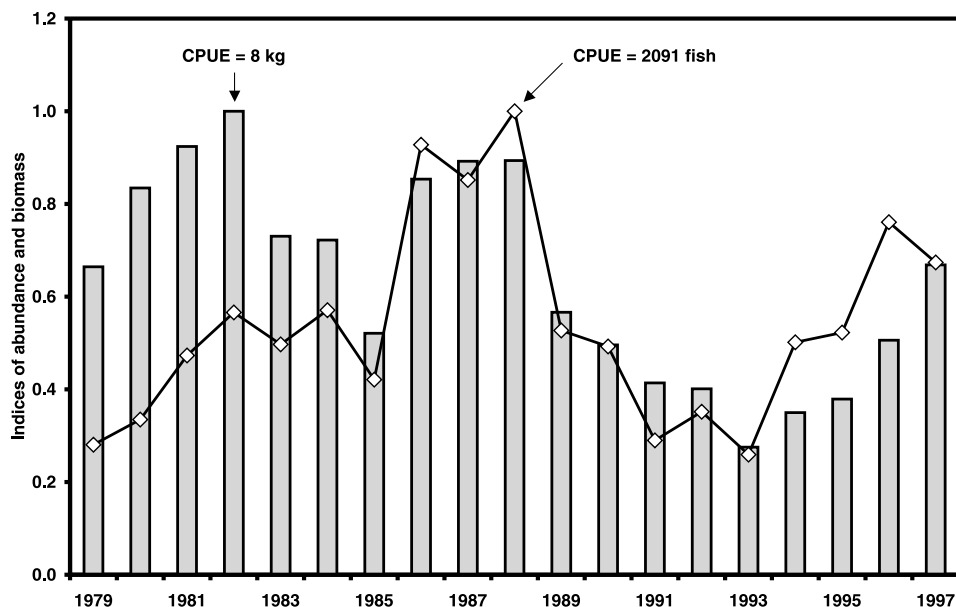
### Threespine stickleback, emerald shiner, and deepwater sculpin

The recent emergence of native fishes like threespine stickleback and emerald shiner reflects a significant change in the Lake Ontario fish community. Owens et al. (2003) suggested that the seminal event that allowed these native fishes to reproduce successfully was a relaxation of predation on their larvae resulting from the shift of alewife to deeper water. Deepwater sculpin, once abundant in the deeper waters of the main basin (Dymond et al. 1929), were not reported in southern Lake Ontario during 1943–1971, and Christie (1973) reported that the last specimen identified from northern Lake Ontario was taken in 1953. Deepwater sculpin were listed by Crossman and Van Meter (1979) as being present in 1972–1975, although they noted that the fish were extremely rare and considered endangered. After 1972–1975, deepwater sculpin were not reported until 1996–1998, when one was caught in the Ontario Ministry of Natural Resources index trawling program in 1996. Thereafter, a few were taken near mid-lake in the northeast (Casselman and Scott 2003), and in 1998, one was caught off the southwest shore, the first sighting of this formerly abundant fish in U.S. waters since 1942. The reappearance of deepwater sculpin in Lake Ontario was the last in a series of changes in the open-water fish community that followed the shift of rainbow smelt and alewives to deeper water in the early 1990s (O'Gorman et al. 2000). The distribution shift coincided with, and was probably a result of, the colonization of Lake Ontario by dreissenids and the concomitant increase in water clarity.

**Fig. 5.** Indices of relative abundance of alewives yearling and older for a 21-year period, 1978 to 1998, caught in trawl tows of 10-min duration in late April – early May in U.S. waters of Lake Ontario ( $\square$ ). Index is a 3-year running mean standardized to the maximum stratified CPUE (catch-per-unit-effort) indicated. Indices of abundance of alewife yearlings and older for a 27-year period, 1972 to 1998, caught in deep-water  $\frac{1}{2}$  nautical mile trawl hauls in the summer months, May–August, in the Canadian Kingston Basin of Lake Ontario (6 sites) ( $\triangle$ ). Index is a 3-year running geometric mean standardized to the maximum CPUE indicated (from Casselman and Scott 2003).



**Fig. 6.** Indices of relative abundance ( $\diamond$ ) and biomass (bars) of age-1 and older rainbow smelt for a 21-year period, 1978 to 1998, caught in trawl tows of 10-min duration in late May – early June in U.S. waters of Lake Ontario. Indices are 3-year running means standardized to the maximum stratified CPUEs (catch-per-unit-effort) indicated.



### Coregonids, blueback herring, and round goby

Remnant populations of lake herring (*Coregonus artedii*) continue to persist in Lake Ontario (Casselman and Scott 2003; Owens et al. 2003), whereas four species of deepwater coregonids that were present in Lake Ontario in the 1960s (Todd and Smith 1992) have disappeared. In 1964, Wells (1969) reported catching bloater (*C. hoyi*), shortnose cisco (*C. reighardi*) and kiyi (*C. kiyi*) in experimental gill nets

along the south shore, but he noted that deepwater coregonids were extremely scarce. Only one deepwater coregonid (bloater) was caught in northwestern Lake Ontario in 1972 (Owens et al. 2003), the next documented catch was in 1983, and thereafter none were caught. Although some native fishes have disappeared in Lake Ontario, two new exotic fishes were reported in the late 1990s, the blueback herring (*Alosa aestivalis*; Owens et al. 1998) and the round

goby (*Neogobius melanostomus*; Charles O'Neill, New York Sea Grant, Brockport, NY 14420, personal communication).

Historically, lake whitefish (*Coregonus clupeaformis*) were an important component of the Lake Ontario commercial fishery and an abundant species in the cold-water fish community of eastern Lake Ontario (Christie 1973; Hoyle et al. 2000). Most of the commercial harvest was taken from the Kingston Basin, where two major spawning stocks exist, a stock that spawns in the Bay of Quinte and a stock that spawns along the south shore of Prince Edward County. By the mid-1960s, these two stocks and the fishery that they supported had collapsed; only a remnant population persisted through the late 1960s and 1970s. Bottom trawling surveys indicated that age-0 lake whitefish production began to increase in the late 1970s (lake stock) and early 1980s (bay stock). After 1986, significant age-0 production was more consistent, as evidenced by large year-classes in 1987, 1991, 1992, 1994 and 1995. Cold fall and winter conditions, followed by more ideal warm summers, combined with the reduction of large rainbow smelt, resulted in a substantial lake whitefish resurgence in the late 1970s and early 1980s (Casselman et al. 1996). By the early 1990s, the stocks had recovered to historically high levels of abundance, and had accumulated a large spawning-stock biomass composed of several strong year-classes (Casselman et al. 1996). Lake whitefish abundance peaked in the early 1990s but declined rapidly after 1992. The deepwater amphipod *Diporeia* has been an important food item of Lake Ontario lake whitefish (Ihssen et al. 1981), and with the collapse of this important food resource in the Kingston Basin by the mid-1990s, lake whitefish shifted to other prey items, notably dreissenid mussels. Associated with the shift in diet to *Dreissena* came a dramatic decline in lake whitefish body condition and their population decline (Hoyle et al. 2003).

### Chinook salmon

The combination of angler preference for large, fast-growing salmon, the desire of fishery managers for a predator that would control large numbers of alewife, and the comparably lower hatchery production costs of chinook salmon led to chinook salmon becoming the key player in the species mix of Lake Ontario's salmonid community. By 1982, chinook salmon was the principal salmonid predator in Lake Ontario and represented between 32 and 54% of annual stocking from 1982 to 1999. Predation by chinook salmon on alewife was so effective that managers became concerned that predator demand might outweigh prey supply. Because of their high abundance and fast growth, chinook salmon accounted for an estimated two-thirds of the lakewide predator demand for alewives (Jones et al. 1993). Consequently, management of predator demand required modification of chinook salmon stocking levels, but because of the popularity of this recreational fishery, changes in stocking levels were controversial. As a result, chinook salmon stocking numbers received considerable attention and public scrutiny in the United States and Canada (O'Gorman and Stewart 1999; Stewart et al. 1999). Stocking numbers peaked in 1984 at 4.2 million fish and ranged from 3.2 to 3.6 million fish from 1985 to 1992. Chinook salmon stocking was reduced substantially during 1993–1994, based on a management review in 1992 (O'Gorman and Stewart 1999), and ranged from 1.5

to 1.7 million fish annually from 1994 to 1996. Because of stakeholder demand and a second management review (Stewart et al. 1999), stocking was increased slightly in 1997 and ranged from 2.0 to 2.2 million fish annually from 1997 to 1999.

### Lake trout

Native lake trout declined to extinction in Lake Ontario by the 1950s (Christie 1973). Hatchery-reared lake trout stocked in the Kingston Basin during 1953–1964 survived well (Pearce et al. 1980), but few survived to sexual maturity because of harvest by commercial gill nets and predation by sea lampreys (Christie 1973). Control of sea lamprey began in 1971 (Elrod et al. 1995), and lake trout stocking was renewed in 1973 with the goal of restoring a self-sustaining population (Schneider et al. 1983). Nine genetic strains were used in the restoration effort, six non-Great Lake strains, two Lake Superior strains, and one mixture of genetic strains of hatchery fish that survived to maturity in Lake Ontario (Elrod et al. 1995). Lake trout stocking increased from 66 000 fish in 1973 to 1.9 million fish in 1985 and was maintained above 2.0 million fish annually until 1992. Changes in stocking policy to reduce predation on alewife (O'Gorman and Stewart 1999; Stewart et al. 1999) resulted in reductions in lake trout stocking in 1993. Management efforts to minimize mortality from sea lampreys, anglers, and commercial fishers and the shift in stocking to mostly Seneca strain (a genetic strain with a higher survival rate than other strains) contributed positively to rebuilding the lake trout population (Marsden et al. 1989; Elrod et al. 1995).

Despite seemingly adequate numbers of mature lake trout through much of the 1980s and into the early 1990s (Selgeby et al. 1995), there were few reports of naturally produced fish except for fry captured on spawning shoals (Casselman 1995; Elrod et al. 1995; Krueger et al. 1995). Failure of the hatchery-origin fish to reproduce was puzzling because many of the factors thought to contribute to reproductive failure of lake trout in the Great Lakes were relaxed, and ecosystem quality seemed to be improving (Fitzsimons et al. 2003). Contaminant levels, which were of great concern for adult lake trout (Huestis et al. 1996) and lake trout fry (Fitzsimons 1995), declined in the 1970s and 1980s. Nutrient levels (Nichols and Hopkins 1993) and excessive periphyton growth, which might cause low oxygen levels in interstitial spaces on spawning reefs during egg incubation (Sly 1988) had declined and were now less likely to impact lake trout recruitment. Alewives, however, were suspected to impede resurgence of lake trout because of their ability to exert heavy predation pressure on lake trout fry (Jones et al. 1995; Krueger et al. 1995) and because of their ability to induce mortality of fry through thiamine deficiency brought about by a maternal lake trout diet of alewife (also known as early mortality syndrome (EMS); Fitzsimons et al. 1999). Although thiamine levels and the resulting EMS were not sufficient to completely block recruitment, the sublethal effects resulting from the thiamine deficiency pose a significant bottleneck to recruitment. Nevertheless, naturally produced age-1 and older lake trout of the 1993–1998 year-classes were found in low numbers throughout U.S. waters (O'Gorman et al. 1998; Owens et al. 2003). Reasons for the abrupt shift from consecutive years of total reproductive fail-

ure to consecutive years of limited reproductive success, as evidenced by nearly 150 young native lake trout caught in U.S. and Canadian waters from 1993 to 1999, are not clear. However, the shift coincided with a peak in potential egg deposition (B.F. Lantry and R. O'Gorman, unpublished data) and a change in the springtime distribution of alewives away from nearshore lake trout nursery areas to deeper water (O'Gorman et al. 2000).

### Walleye, yellow perch, and smallmouth bass

Walleye (*Stizostedion vitreum*) is an important keystone predator of the inshore fish community of eastern Lake Ontario and the associated embayments. Walleye reached record-setting high levels in the Bay of Quinte in the early 1990s. This increase occurred as the result of a major resurgence in the late 1970s after the population had been at record-setting low levels in the early 1970s. The resurgence began as a result of an extremely large year-class in 1978 after the winterkill of its larval predators, alewife and white perch, which occurred after the severe winters of 1976–1977 and 1977–1978 (Casselman and Scott 2003). In the late 1980s and early 1990s, the walleye population of the Bay of Quinte moved down the bay as spawning runs of alewife, an important prey species for walleye, diminished. Although large walleye have seasonal migrations between the Bay of Quinte and eastern Lake Ontario, this shift, along with the increased abundance of walleye, initiated their dispersion out of the lower Bay of Quinte into eastern Lake Ontario. This was accelerated in the early 1990s by the progressively increasing transparency caused by dreissenid colonization (Casselman and Scott 2003). In the mid-1990s, walleye abundance increased in New York waters of Lake Ontario's eastern basin. This increase, which was also seen in the upper St. Lawrence River, no doubt reflected the dispersion of the Bay of Quinte stock. Coincident with this decrease, yellow perch (*Perca flavescens*) abundance increased substantially throughout the Bay of Quinte at a time when the species was generally decreasing in the eastern basin of Lake Ontario in both New York and Ontario waters.

Yellow perch were at record-setting high levels in north-eastern Lake Ontario in the late 1970s and early 1980s but declined precipitously in the mid-1980s. Among the many factors associated with these dynamics was a massive winterkill of alewives, significant predators of yellow perch larvae (Mason and Brandt 1996), in the late 1970s followed by a strong rebound in the 1980s. A shift in alewife distribution in the early 1990s boosted yellow perch reproductive success, but it was followed by increased double-crested cormorant (*Phalacrocorax auritus*) predation that appears responsible for decreasing yellow perch abundance in eastern Lake Ontario in recent years (Burnett et al. 2002). In unison, smallmouth bass (*Micropterus dolomieu*), which were at record-setting high levels in the late 1970s, 1980s, and early 1990s throughout the eastern basin of Lake Ontario, also reached record-setting low levels in the late 1990s, with some weak recovery. This decrease has been associated with cormorant predation in both U.S. and Canadian waters (Lantry et al. 2002; Casselman et al. 2002). Some of the poorest year-classes seen in decades occurred in the early 1990s as a result of several extremely cold summers, especially in 1992 as a result of the Mount Pinatubo eruption in 1991

(Casselman 2002). Even though recruitment conditions were especially good in the late 1990s, particularly in the extremely warm summers of 1995 and 1998, smallmouth bass abundance has not shown any significant resurgence.

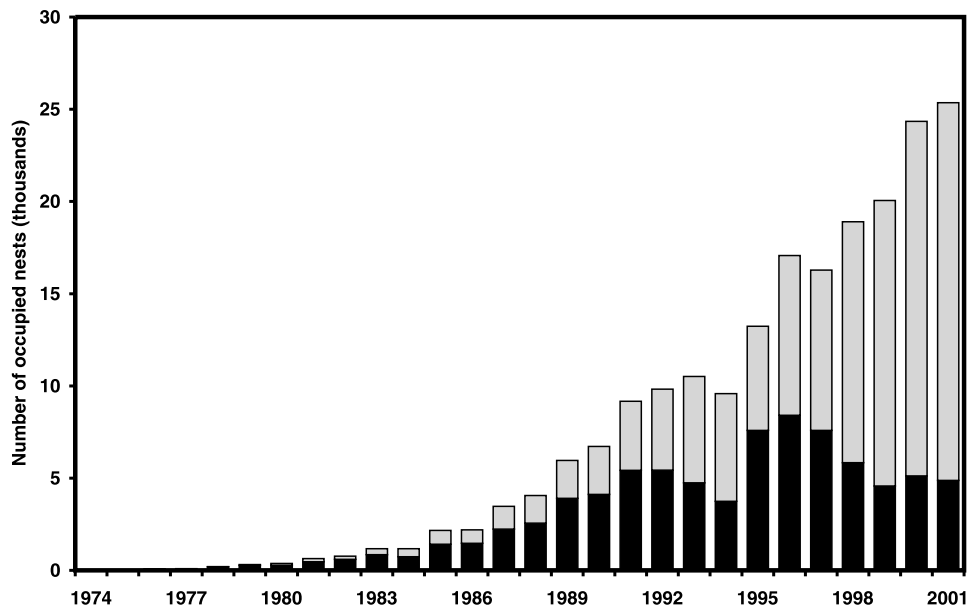
### Double-crested cormorants

Double-crested cormorants were first observed in Canadian waters of Lake Ontario in 1938 and in New York waters of Lake Ontario in 1945 (Weseloh and Ewins 1994). Breeding numbers remained low until the late 1970s mainly because of contamination of Lake Ontario by organochlorine compounds, particularly DDE (dichlorodiphenyldichloroethylene), which resulted in thinning and breakage of eggshells and reproductive failure (Weseloh 1987). The combination of reduced levels of DDE, augmented by an abundant food supply (primarily alewife), and their protected status in both the U.S. and Canada led to a dramatic resurgence of double-crested cormorants in the 1980s and 1990s. The number of nests occupied by cormorants on Little Galloo Island (LGI) in eastern Lake Ontario and numbers of the Lake Ontario population increased dramatically after 1974 (Fig. 7). LGI nest numbers continued to increase through 1996, after which they declined in response to intense human activity associated with pellet collections and eventually egg oiling. Reproductive output and survival of cormorants appears to be tightly linked with alewife abundance; years with abundant alewife populations have also been years of high postfledging survival of these birds (Weseloh and Ewins 1994). Although cormorants seemingly have had little overall effect on alewife stocks, subsequent studies in U.S. waters of the eastern basin of Lake Ontario indicated adverse impacts on smallmouth bass (Lantry et al. 2002) and yellow perch (Burnett et al. 2002).

### The Lake Ontario food web

Ecological changes in the Lake Ontario food web have been dramatic since SCOL I (Fig. 8). In the decades of the 1950s and 1960s, pessimism prevailed among Great Lakes scientists and managers as depredation of the fish communities and degradation of water quality proceeded unabated. By 1970, lake trout populations were gone; the few remaining salmonids were riddled with sea lamprey wounds; cultural eutrophication resulted in excessive algal growth and low water clarity; proliferation of alewife led to intense zooplanktivory and a predominance of small cladocerans and cyclopoid copepods; and only a remnant population of lake whitefish persisted (Figs. 8a and 8b). In ensuing years, oligotrophication would drive the recovery process and the food web would be greatly altered (Figs. 8c and 8d). In 2000, sea lamprey predation no longer plagued salmonids and burbot, exotic alewife supported a Pacific salmon recreational fishery, and invasion of *Dreissena* spp. fostered new trophic interactions. The microbial food web, including bacteria, ciliates, heterotrophic nanoflagellates, and picoplankton, was identified as an essential pathway of energy transfer to zooplankton in 2000, but less so in 1970. Food web changes were most evident in the nearshore: *Diporeia* disappeared, seven new invasive species were established (*Cercopagis*, zebra and quagga mussels, round goby, New Zealand mud snail, blueback herring, and *Echinogammarus*), fingernail clams disappeared, double-crested cormorant populations

**Fig. 7.** Numbers of double-crested cormorant nests on Little Galloo Island (solid) and elsewhere (shaded) in Lake Ontario, 1974–2001 (after Weseloh and Ewins 1994; D.V. Weseloh, Canadian Wildlife Service, 4905 Dufferin Street, Downsview, ON M3H 5T4, and I.M. Mazzocchi, New York State Department of Environmental Conservation, 317 Washington Street, Watertown, NY 13601, personal communications).



greatly expanded, and water clarity increased dramatically. In offshore waters, quagga mussels dominated over zebra mussels, and *Cercopagis* proliferated in late summer and early fall. Despite these changes, omnivorous *Mysis* populations remained relatively stable, coupling the benthic and pelagic food webs.

## Discussion

Fisheries exploitation, exotic species introductions, and eutrophication were highlighted in SCOL I as factors contributing to the degradation of the Great Lakes fish communities. Sea lamprey and the alewife were recognized as particularly important predators impacting the Lake Ontario fish community (Christie 1972; Christie et al. 1987b). Since 1970, negative effects of exploitation on native fishes, eutrophication, sea lamprey, and alewife have been largely ameliorated, thereby contributing greatly to restoration efforts in Lake Ontario. However, establishment of new non-native species continues to hamper goals to restore Lake Ontario's historic fish communities, and the resultant ecological effects may be irreversible.

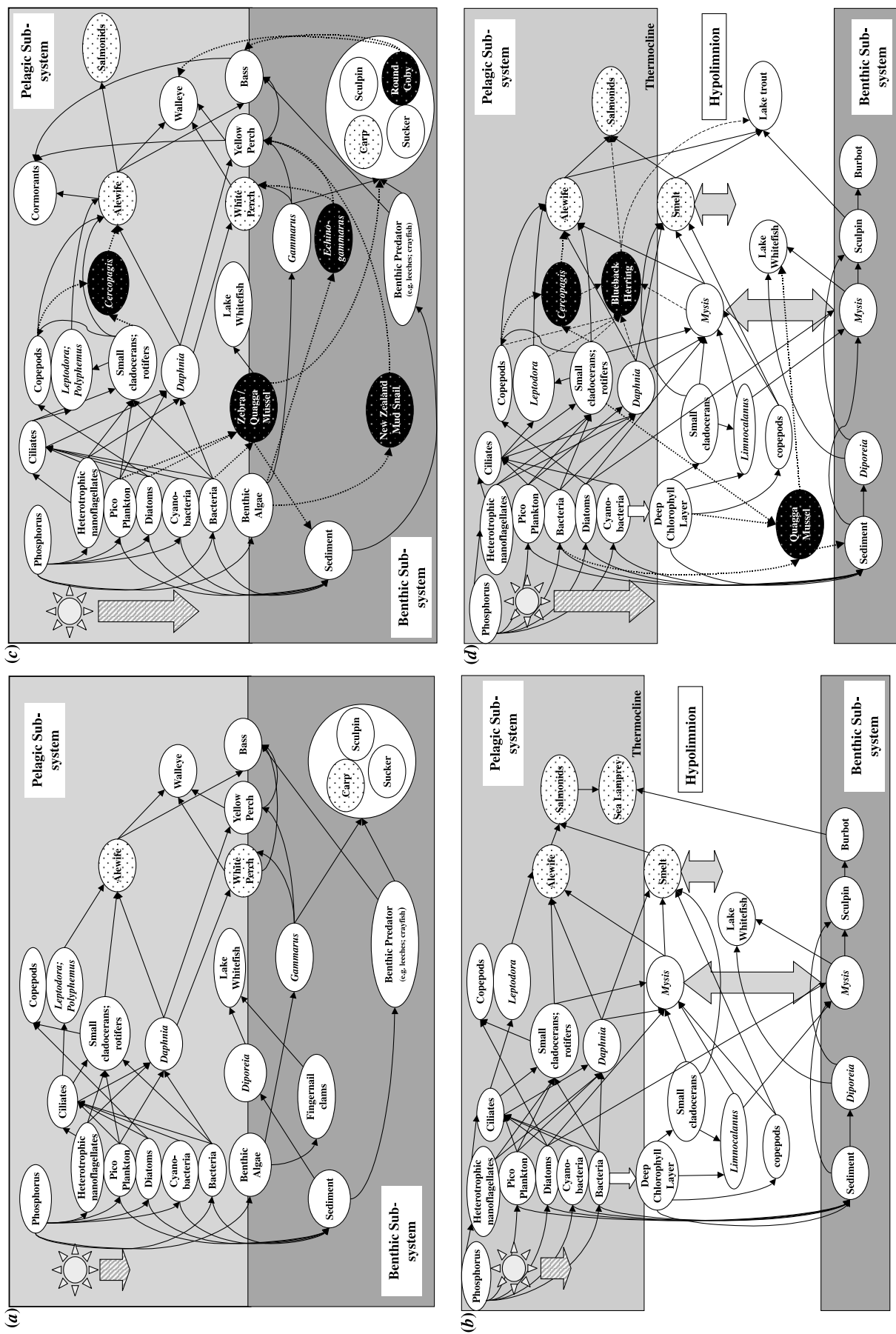
Managers of the Lake Ontario ecosystem in the late 1960s and early 1970s recognized that water quality degradation was so extreme that the lake environment had to be changed, but that there were no guarantees of success. Results of ecological studies indicated that eutrophication could be reversed through mandated controls on phosphorus loading to the lake (Neilson and Stevens 1987). The GLWQA signed by the U.S. and Canada in 1972 provided the backdrop to reduce total phosphorus levels in offshore waters of Lake Ontario to a target level of  $10 \mu\text{g}\cdot\text{L}^{-1}$  and set the stage for oligotrophication. Skeptics predicted that environmental change was either irreversible or would take decades, but Lake Ontario (and Lake Erie) responded soon after remedial measures were in place. What was not appreciated at the

time of the GLWQA, however, was the connection between phosphorus supply and higher trophic level production, especially to fish. Subsequently, scientists realized the need for long- and short-term studies that focused on food web linkages and managers recognized their value in decision-making. Scientists and managers would take longer to acknowledge that the issues of water quality and fisheries production were linked.

Control of the sea lamprey was effective in improving survival of salmonid piscivores in Lake Ontario, and advances in fish culture technology made it possible to establish large populations of salmonid predators that were effective in controlling alewife. With an expanding salmonid predator population, fish managers were forced to address ecological issues related to food availability, habitat, genetics, disease pathogens, and exotics, as well as the concerns of the stakeholder public.

Managers hoped that the path to recovery of the Lake Ontario ecosystem following the 1950s and 1960s would be a return to historic conditions. Early signals were consistent with this expectation. For example, nuisance algal blooms dramatically declined, and native species like lake trout responded positively to nutrient abatement and sea lamprey control (Elrod et al. 1995). Further, structural changes in the size and species composition of phytoplankton indicated a shift from a eutrophic to an oligotrophic community, and associated with this change, smaller-sized organisms contributed more to primary productivity (Munawar and Munawar 2003; Munawar et al. 2003). However, the recovery of Lake Ontario would take a new ecological path — one that would be markedly influenced by unplanned exotic species introductions. Restoration of lake trout, for example, would be hampered by a thiamine deficiency of the fry brought about by adult lake trout feeding on non-native alewife (Fitzsimons et al. 1999). Lake whitefish populations would no longer thrive because of

**Fig. 8.** The food web of Lake Ontario in (a and b) 1970 and (c and d) 2000. Thin solid arrows indicate the direction of energy flow, thin dotted arrows represent energy flow to and from exotic species introduced since 1970, wide bidirectional arrows represent migration through the water column, and wide unidirectional arrows represent relative depth of light penetration. All exotic species are stippled, and those that arrived post-1970 are dark stippled. Predator-prey interactions involving larval fish are not depicted.



the loss of their preferred food, the native burrowing amphipod *Diporeia*. The lesson of the last three decades has been clear: the trajectory of the recovery process of the Lake Ontario food web has taken new and unpredicted ecological paths.

Restoration of Great Lakes native fish communities has often been considered a signal toward the return to a healthy ecosystem. Re-establishment of the bloater into Lake Ontario would satisfy those who desire an ecosystem that supports a self-reproducing diverse fish community. Historically, bloater populations developed migration patterns in close association with their migrating prey, *Mysis*. Mysids are abundant in Lake Ontario's abyss; offshore biomass of *Mysis* can exceed that of alewife and rainbow smelt combined (Johannsson et al. 2003). The lack of a significant deepwater predator on *Mysis* is a missing link in the Lake Ontario food web, a link that limits movement of energy in the offshore pelagia. Evidence of improved environmental conditions, reduced alewife and rainbow smelt densities, and an abundant offshore mysid population in Lake Ontario would seemingly provide a window of opportunity to re-establish bloaters. However, collapse of *Diporeia* has eliminated the likelihood of fully restoring bloater because *Diporeia* was the most important food in bloater diets, followed closely by *Mysis* (Wells and Beeton 1963). Although competition for food with dreissenids is suspected as the cause for collapse of *Diporeia*, other factors like disease from pathogens are also possible. If mysid populations collapse, restoration of bloater to any level of abundance would be impossible.

Concerns about the role of persistent organic contaminants on the demise of lake trout in Lake Ontario and continued prevention of successful rehabilitation when reintroduced to the lake in the 1970s have persisted for decades (Zint et al. 1995; Cook et al. 1997). The suspected historic causality of contaminants on lake trout mortality can never be definitively determined because we have only recently seen the development of the appropriate analytical methods to detect and quantify such contaminants. Nevertheless, new methodologies and assessment techniques (Cook et al. 1997) now permit much more definitive statements of the current potential of contaminants to block fish reproduction (Fitzsimons 1995). The effects of contaminants on lake trout and other fish species will continue to evolve in the coming decades. Although larval lake trout are highly sensitive to dioxin and dioxin-like chemicals, residue levels are now below those associated with acute toxicity. The synergistic effects of these other organochemicals on newly discovered phenomena like diet-induced thiamine deficiency (Fisher et al. 1996; Fitzsimons et al. 1999) on fish, for example, is unknown but needs to be explored.

One of the most dramatic changes in the Lake Ontario ecosystem since SCOL I was improved water clarity resulting from both oligotrophication and the invasion of dreissenids. Increased water clarity has resulted in far-reaching trophic interactions that could have profound effects on predator-prey interactions. For example, food availability of visual predators may be influenced more by changes in light regime than by changes in food abundance. In addition, water clarity changes may also modify the behavior of organisms and their impact on the food web. Following the establishment of dreissenid mussels in Lake Ontario, increased water

clarity may have caused alewife, rainbow smelt, and age-2 lake trout to shift to deeper water (O'Gorman et al. 2000). The outcome of this shift to deeper waters is currently unclear; we can only speculate that this behavior modification will increase predation on *Mysis*.

Zebra mussel-induced water clarity changes likely redirected nearshore energy production to the benthic habitat and perhaps made this habitat more vulnerable to invasion by other non-native species. So far, *Echinogammarus*, the New Zealand mud snail, and the round goby have become established in nearshore benthic habitat during the 1990s. Round gobies will likely play a special role in the coming decades by functioning as a benthic prey and an energy vector between *Dreissena* spp. and other fish species, especially with the current declines in *Diporeia* and slimy sculpins. Gobies, however, are unlikely to replace slimy sculpins as the preferred prey of juvenile lake trout during thermal stratification because bathymetric distributions of the two species differ, gobies on bottom above the thermocline and juvenile lake trout on bottom well below the thermocline. However, if gobies migrate to greater depths in fall as thermal stratification weakens, they will likely provide food for juvenile and adult lake trout and, as such, would partly fill the functional role of slimy and deepwater sculpins. Interestingly, future food web scenarios for Lake Ontario will no doubt ponder organism functionality: does it matter whether lake trout feed on gobies or sculpins if these benthic fishes serve similar functional roles in the food web?

In spite of dramatic ecological changes in the Lake Ontario ecosystem since 1970, *Mysis* populations have exhibited little response to oligotrophication (not surprising considering its origins in the Great Lakes as a glacial relict), increased water clarity, and top-down effects of fisheries management. In contrast to zooplankton, *Diporeia*, and alewife, *Mysis* have shown no trend in abundance over time. However, *Mysis* production has increased, due possibly to declines in larger alewife, which feed on *Mysis* (Johannsson et al. 2003). This low level of response of the mysid population could be due to their migration patterns and their use of a habitat that by volume is the largest in the lake. Combined, these factors effectively minimize predation on *Mysis* from visually feeding fish. In addition, omnivory allows *Mysis* to switch to algae or detritus if their primary zooplankton prey declines. The main importance of *Mysis* for alewife, the primary forage fish in the lake, may be one of energy storage (Johannsson et al. 2003), as metalimnetic zooplankton production can be stored as mysid biomass and fed on by alewife from fall through spring when distribution of the two species overlap. The consequence of the availability of *Mysis* as food for alewife in the fall could have significant implications for their growth, gonad development, and overwinter survival.

## Moving into the future

The post-1970 era provided assurance to skeptics that environmental change in the Lake Ontario ecosystem associated with chemical pollution was reversible. What was not so surprising from the lessons learned over the past 30 years in Lake Ontario was that environmental change associated with biological pollutants like invasive species is likely irreversible. Once established, exotics rarely disappear although

their role in the food web may change significantly. For example, the role of the alewife has shifted over the last six decades from a nuisance species to a pivotal species that supports a multimillion dollar salmonid sport fishery (O'Gorman and Stewart 1999). Ironically, although environmental conditions have greatly improved in Lake Ontario and the other Great Lakes since 1970, this period has coincided with an acceleration of newly established exotics (Mills et al. 1993). Global transport of organisms associated with shipping and the establishment of organisms from distant places like the Black, Caspian, and Baltic seas were unheard of in the decades prior to 1970. Although the intent of the U.S. – Canada Water Quality Agreement was “to restore and maintain the chemical, physical, and biological integrity of Great Lakes waters”, release of untreated waters from the ballast tanks of foreign vessels into the Great Lakes was not considered within the mandate. We anticipate that future policy efforts will institute measures that will reduce the risk of introducing new biological pollutants to Lake Ontario and other Great Lakes.

Over the last two decades, Lake Ontario has experienced significant reductions in phosphorus with a concomitant shift toward oligotrophy and a dramatic increase in water clarity resulting from both nutrient reduction and proliferation of filter-feeding *Dreissena* spp. Macroinvertebrate activity has increased since invasion by *Dreissena* spp. (Stewart and Haynes 1994), light penetration has increased, benthic-feeding round gobies have become established, and benthic algae like *Cladophora* have reportedly reached nuisance levels again (Charles O'Neill, New York Sea Grant, Brockport, NY 14420, personal communication). We suggest that these events are in response to greater light penetration and reflect a redirection of energy production from the pelagic to the benthic habitat. We contend that the combined effects of oligotrophication and dreissenid-induced modifications will favor benthic over pelagic energy pathways, particularly in nearshore and embayment habitats of Lake Ontario. We expect that this shift in the direction of energy flow will have dramatic ecological consequences for Lake Ontario in the future by favoring colonization of bottom-dwelling organisms, promoting fish communities that make efficient use of the benthic habitat, and enhancing growth rate cycles of benthic algae and submersed aquatic vegetation. Thus, we expect this shift in importance of benthic processes (termed benthification) to be coupled with the oligotrophication of Lake Ontario.

The role of climate and global climate warming are new stressors that were not identified in SCOL I. Summer and early winter inshore water temperatures have increased significantly in Lake Ontario over the past several decades, paralleling global warming and temperature extremes, particularly those associated with El Niño and La Niña (Casselman 2002). We expect that future global warming will lead to increasing water temperatures in Lake Ontario and thereby affect fish community dynamics and their habitat. Global warming's impact on fish species may be either positive or negative depending on species-specific thermal requirements and changes in thermal habitat. Rising temperatures associated with seasonal climate events could positively affect salmonids by increasing the habitat volume for cold-water species in well-oxygenated lakes like Lake Ontario (Magnuson et al. 1990). On the other hand, in-

creasing water temperatures in late fall and early winter may negatively affect fish survival and fry emergence, notably of lake trout and lake whitefish (Casselman 1995). At the same time, increasing water temperature could result in stronger year-classes of warmwater species such as smallmouth bass (Casselman et al. 2002) and alewife.

The initial introduction of salmonids into the Great Lakes was an attempt to control nuisance levels of alewife but quickly focused on developing a multimillion dollar recreational fishing industry (O'Gorman and Stewart 1999). The strategy for rehabilitation of lake trout, and later Atlantic salmon, in Lake Ontario had strong scientific and ecological underpinnings (Schneider et al. 1983; Elrod et al. 1995). However, the overwhelming desire of stakeholders to have a recreational fishery made up of naturalized and exotic salmonids has been the driving force of fish management to date. Consequently, the current Lake Ontario fish community is largely composed of a mix of exotic species that have no evolutionary sympatry. In addition, control of these salmonids and their associated top-down influence on fish communities (Christie et al. 1987a; McQueen et al. 1989) is largely regulated through stocking. As a result, conventional ecological paradigms are difficult to apply, and descriptions of historical fish community structures are not useful for understanding or predicting species interrelationships or equilibrium states (Christie et al. 1987b; Eshenroder and Burnham-Curtis 1999). Managers of the Lake Ontario fishery resource will be challenged in the coming decades as the ecosystem changes and will need to rely on the use of such tools as ecological modeling and risk assessment to gain insights into outcomes and consequences of management decisions.

Multiple biological and physical stressors have caused profound changes in the Lake Ontario ecosystem and its fish community during the last three decades. Major stressors over this period included oligotrophication, invasion by dreissenids that led to increased water clarity and benthification, fisheries management through stocking of exotic salmonids and lamprey control, climate change, establishment of other exotics, and harvest by anglers and cormorants. Responses to these stressors have led to significant changes in the fish community, including declines in alewife, declines in native sculpins and lake whitefish populations, increases in some native fishes associated with lamprey control, shifts in alewife spatial distribution, and declines of fish species resulting from double-crested cormorant predation. In addition, fish recruitment bottlenecks have resulted from alewife-induced thiamine deficiency. We expect stressor impacts to continue to shape the Lake Ontario ecosystem in the future and recommend continuous long-term ecological studies to enhance scientific understanding and management of this important resource.

As we move into the future, we will continue to wrestle with the more global issue of sustainability of fishery resources. Some will argue for maximum utilization of the fishery resources, and others will be more concerned with further restoration of native, natural species assemblages. Regardless of which fish community type is preferred, understanding how fish integrate into the Lake Ontario food web and respond to environmental change has become embedded in the thinking of managers and scientists alike. The



Lake Ontario ecosystem and its stakeholders have and will continue to profit from this philosophy in the coming decades. The Lake Ontario food web and energy partitioning within the food web has become more complex, particularly in the nearshore waters. Understanding ecological processes involving benthic and pelagic food web pathways and their linkages to fish will continue to challenge both our scientific understanding and desire to manage large-lake ecosystems. The challenges for scientists, managers, and stakeholders in the coming decades will be monumental, as expectations will be hampered by ecological surprises resulting from anthropogenic forces like climate warming and exotic species invasions. We hope that society will invest in the future of Lake Ontario and other Great Lakes as they are some of the greatest natural resources on earth.

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